

INTERSPECIFIC AND INTRASPECIFIC ACORRHAGIAL AGGRESSIVE BEHAVIOR AMONG SEA ANEMONES: A RECOGNITION OF SELF AND NOT-SELF

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Coelenterates have long been considered primitive or simple animals. Although some aspects have been known for a long time, coelenterate behavior and its physiological and morphological bases are still poorly understood. Studies have now shown coelenterates to be capable of a variety of fairly complex behaviors, including aggression (Pantin, 1952; Francis, 1973b; Ross, 1974).

All sea anemones possess tentacles, the interior of which are continuous with the digestive cavity (coelenteron). In addition, some species have other "hollow" structures, such as the acrorhagi. Although acrorhagi were first described by Rapp in 1829, as small, light-blue buttons on the rim of the disc of *Actinia mesembryanthemum* (= *Actinia equina*), the function of these structures remained a mystery until the middle of this century.

Based on morphological evidence alone, functions attributed to the acrorhagi included photoreception (Hollard, 1851; Duncan, 1874), sensitivity to touch (Korotneff, 1876), and defense (Gosse, 1860). Neither the Dixons (1891), who gave one of the first accounts of the behavior associated with acrorhagi, nor Walton (1910) perceived the importance of their observations concerning the acrorhagi. It remained for Abel (1954) to recognize the significance of and more completely describe the acrorhagial response of sea anemones.

Abel (1954), Bonnin (1964), Francis (1973b), Bigger (1976), Williams (1978), and Brace and Pavey (1978) have reported the same basic acrorhagial behavior in five species of sea anemones. After an acrorhagi-bearing animal touches some conspecifics, or certain other coelenterates, the acrorhagi in the area of contact swell and elongate. The expanded acrorhagi are placed on the other animal, withdrawn, and then the application process is repeated. Pieces of the acrorhagial ectoderm (acrorhagial peels) remain on the target animal. Within as little as 20 min (Bonnin, 1964), the tissue of the target animal receiving the peel exhibits signs of necrosis. The acrorhagial response with its directed nature and infliction of injury has been considered an aggressive behavior (Francis, 1973b) and, thus far, has established sea anemones as the "simplest" animals to possess aggressive behavior.

Francis (1973a, 1976) established competition for space as a possible ecological role for the acrorhagial response and demonstrated an intracolonial division of labor between sexual reproduction and acrorhagial aggression in *Anthopleura elegantissima*. Recently the possible relationship of the acrorhagial response to immunocompetence has been discussed (*e.g.*, Hildemann *et al.*, 1975).

This present study further examines the acrorhagial response of four species of sea anemones, two not previously examined, and in particular inquires into

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the nature of inter- and intraspecific relationships and the question of a possible "immunocompetence."

MATERIALS AND METHODS

Animal collection and maintenance

The specimens of *Anthopleura krebsi* used in this study were collected intertidally from a series of rock groins 84 m apart on the sandy substrate of Coquina Beach, Anna Maria Island, Florida. *Anthopleura krebsi* was identified in accordance with Carlgren and Hedgpeth (1952). The anemones, lining crevices and depressions in the rocks, were collected from aggregations of contacting individuals. Although there were various color patterns, the specimens of *A. krebsi* could be generally classified into two color morphs, red or green. All the acrorhagi tips of an individual were the same color, a shade of red or green. In the laboratory, *A. krebsi* commonly reproduces asexually; thus, the anemones in the field aggregations could have been clonemates. However, the term "groupmates" will be used for the anemones from the same aggregation and the term "clonemates" will be reserved for those anemones known, by direct observation, to have the same genotype as a result of asexual reproduction. The specimens of *A. krebsi* ranged in size from 0.5- to 2-cm pedal-disc diameter.

The anemones were transported to Florida State University where they were maintained, individually, by group, or as clones; in culture dishes, fingerbowls, or filtered aquaria. The natural sea water in the dishes was changed every other day.

Anthopleura xanthogrammica was observed at Victoria, British Columbia, and near the Bamfield Marine Station on Vancouver Island, Canada, during an extremely low tide. *Anthopleura xanthogrammica* tended to be solitary and was found in high-tide pools.

The anemone *Bunodosoma cavernata* was collected from the jetties at the Mayport Naval Station, Mayport Beach, Florida. The anemones occurred alone, or in aggregations among the large rocks of the jetty. When collected, specimens of *B. cavernata* ranged in size from 1.5- to 4.5-cm pedal-disc diameter. They were maintained in 5- or 15-gal filtered aquaria containing natural sea water.

The anemone *Anemonia sargassensis* was collected from the rock jetties of the inlet to St. Andrews Bay, Panama City, Florida. The pedal disc diameter ranged from 1 to 2.5 cm. Although they reproduced asexually by longitudinal fission, clones were not isolated and all specimens of *A. sargassensis* were maintained in the same 15-gal filtered aquarium.

Polyps of the scyphozoan *Cassiopea* from the Florida Keys have been maintained in the laboratory at Florida State University since 1974. After the work reported by Bigger in 1976, medusae were raised from the scyphistomae (polyps) and the species identification was confirmed as *Cassiopea xamachana* (Bigelow, 1900). Clones of *C. xamachana*, including both scyphistomae and medusae, were maintained in separate aquaria making it possible to test the reaction of *A. krebsi* to medusae and scyphistomae from the same clone.

All aquaria were provided with sub-gravel filters and some had additional external glass-wool filters. Illumination was provided by Gro-lux fluorescent lights on a 14:10 light:dark regime. The anemones' diet consisted of pieces of shrimp, beef liver, and newly hatched *Artemia* nauplii from San Francisco Bay Brand eggs; while the *Cassiopea* diet consisted of *Artemia* nauplii. Feeding was stopped 3 days prior to and during an experiment.

Behavior and physiology

Except for filmed interactions, all anemone behavior was viewed through a Wild M5D stereomicroscope. The same rheostat setting on the top-mounted lights was used for all trials to maintain constant lighting conditions. Temperatures during observational periods ranged from 20° to 23°C. Behavioral observations were usually made on anemones in their culture dishes. One hour before each experiment, the natural sea water was changed and the animals were placed on the microscope with the lights on to allow them time to adjust. For the behavioral interactions, both animals were allowed to become well expanded before they were moved into contact. The outcome was recorded with still and motion pictures using Nikon FTN (35 mm), Nizo (Super 8 mm), and Bolex (16 mm) cameras; with an Esterline Angus 190-MT event recorder; or by using a stop watch and hand counter with handwritten notes.

To provide more control over the eliciting stimuli, a 1-sec touch technique was used. For this technique an object, such as an excised tentacle or glass coverslip, was lightly touched to an anemone for about 1 sec every 30 sec. Successive contacts were made with the same area on the anemone, and unless otherwise stated, involved a group of four adjacent tentacles. This procedure was continued for 15 min, or until an acrorrhagial response occurred. If acrorrhagial expansion occurred within the 15 min, the contacts were continued until the rest of the response was elicited. As discussed below (Fig. 9), more than 97% of normal interactions occurred within 15 min. An acrorrhagus was considered to be expanded when it enlarged to $\frac{1}{2}$ the length of adjacent tentacles.

Excised tentacles of *C. gigantea* and *A. sargassensis* were used to investigate short term changes in the thresholds of acrorrhagial expansion and application in *A. krebsi* with repeated target contacts. The threshold was defined as the number of touches, using the 1-sec touch technique with an excised tentacle, required to elicit the response from the specimen of *A. krebsi*. In this experiment, the threshold was determined, a period of time was allowed to elapse, and the threshold was determined again for up to 10 determinations. The time intervals used were 10 min for the *C. gigantea* stimulus and 15, 30, 60, and 120 min for the *A. sargassensis* stimuli.

RESULTS

Behavioral alternatives to the acrorrhagial response

During anemone encounters, observable acrorrhagial responses occurred only after physical contact between the anemones. Usually, the contact was initially made by the tentacles and resulted either in an interlacing of the tentacles of both animals with no change in behavior, or a rapid withdrawal of the tentacles of one or both animals. Generally all the tentacles, but often only the tentacles in the area of contact, were withdrawn. The anemones then re-extended the tentacles and the process was repeated until one of three events occurred: 1) after several tentacular withdrawals, the tentacles of the two anemones interlaced and each animal treated the other as an inert object; 2) one or both anemones avoided contact with the other individual; 3) the acrorrhagial response was initiated by one or both anemones.

Anemones avoided contact with other anemones by bending the column away, only partially expanding the tentacles on the side of contact, using the pedal disc to

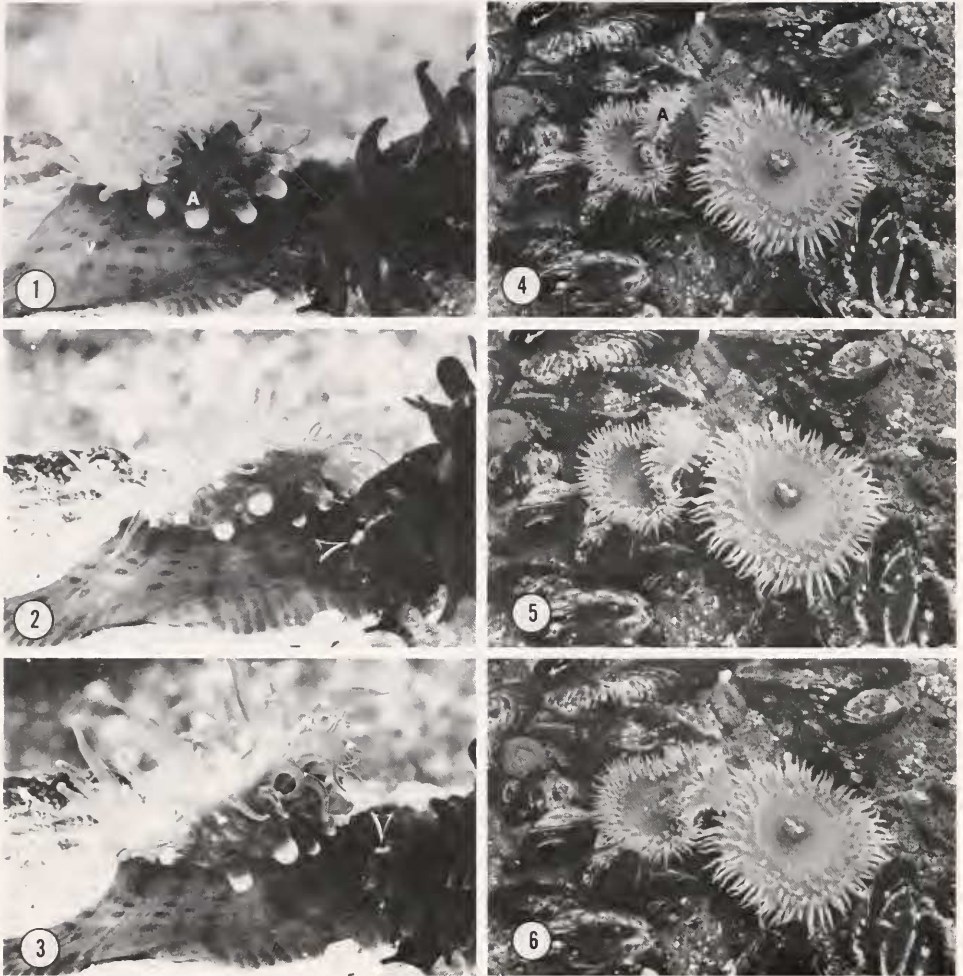


FIGURE 1. The specimen of *Anthopleura krebsi* is in the process of applying its expanded acrorhagi on the target, *A. sargassensis*. A—acrorhagi, V—verruca.

FIGURE 2. The specimen of *Anthopleura krebsi* has just withdrawn its acrorhagi from the target, *A. sargassensis*. The arrow points to an *A. krebsi* ectodermal peel adhering to the target. Note the corresponding "clear" area on the *A. krebsi* acrorhagus tip from which it originated.

FIGURE 3. Following peel (arrow) application by *Anthopleura krebsi* the target anemone, *A. sargassensis*, retracts the afflicted tentacle.

FIGURE 4. The specimen of *Anthopleura xanthogrammica* on the left has expanded its acrorhagi (A) adjacent to the *A. xanthogrammica* on the right.

FIGURE 5. The left specimen of *A. xanthogrammica* is in the process of applying its expanded acrorhagi to the right *A. xanthogrammica*. Note the capitulum is also expanded.

FIGURE 6. The left specimen of *A. xanthogrammica* is applying its expanded acrorhagi to the other specimen of *A. xanthogrammica*.

creep away, and releasing the pedal attachment to the substrate. Under the experimental conditions of this study, an unattached anemone remained in the same general position and contact with the other anemone was not avoided. However, in the field the wave surge or current in all *A. krebsi*, *B. cavernata* and *A. sar-*

gassensis habitats would quickly remove an unattached anemone. Moving away and releasing the hold on the substrate were by far the most common responses of specimens of *A. sargassensis* to other species of anemone and to the predatory nudibranch *Spurilla neapolitana*. *Bunodosoma cavernata* responded to *S. neapolitana* by releasing its hold on the substrate. It also withdrew its tentacles and greatly inflated its column. Inflating the column and floating free are two common anemone responses to nudibranch predation (Edmunds *et al.*, 1976).

Another anemone response to encounters with other animals was predation. Such responses to other coelenterates were of particular interest. Although in some cases feeding behavior and the acrorhagial response were elicited by the same species (Table II), the two behaviors were mutually exclusive. One or the other occurred, but never feeding and the acrorhagial response during the same encounter.

The general acrorhagial response

The five general phases of the acrorhagial response in *A. krebsi*, *A. xanthogrammica* and *B. cavernata* are similar to those found in other actinians (Francis, 1973a, b; Bonnin, 1964): 1) excitation, contact and tentacular withdrawal; 2) acrorhagi expansion (Figs. 1 and 7); 3) application, with the acrorhagi directed to the area of stimulation (Figs. 2, 4, 5, and 8); 4) acrorhagial peeling, discharge of nematocysts and adherence of acrorhagial ectoderm to the target (Figs. 3, 6, and 5) recovery, return to normal posture. Cytological and ultrastructural examinations of the acrorhagus and events of the acrorhagial response are contained in separate reports in preparation.

Anthopleura krebsi acrorhagial response

The excitation period was defined as the time from first contact of the animals to the acrorhagial expansion. Its duration is variable, particularly depending on the species eliciting the response. *A. krebsi* intraspecific response excitation periods varied from 20 sec following a single contact to 25 min, with a mean of 4.9 min (Fig. 9). On the other hand, no responses were elicited by *Cassiopea* in less than 3 min. As in *A. equina* (Bonnin, 1964), *A. krebsi* tentacles in the region of acrorhagi expansion usually deflate as the acrorhagi expand. Many times, how-

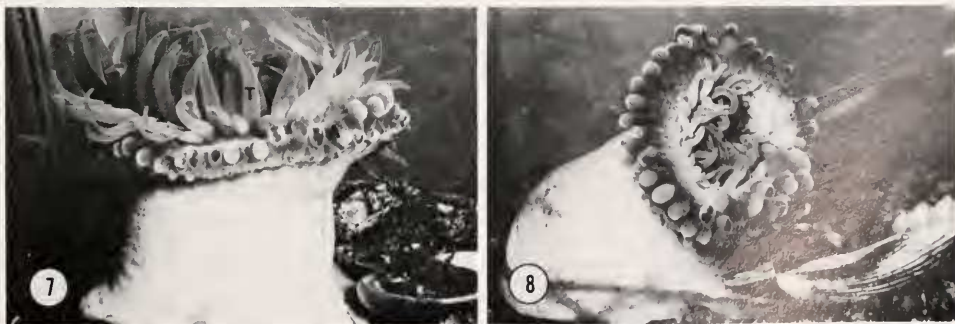


FIGURE 7. *Bunodosoma cavernata* acrorhagi (A) are starting to expand and the tentacles (T) are being drawn into the oral area. Peels were missing from some acrorhagi due to a previous response.

FIGURE 8. *Bunodosoma cavernata*: Note the tentacles held in the oral area and prominent acrorhagi around the oral disc during application behavior.

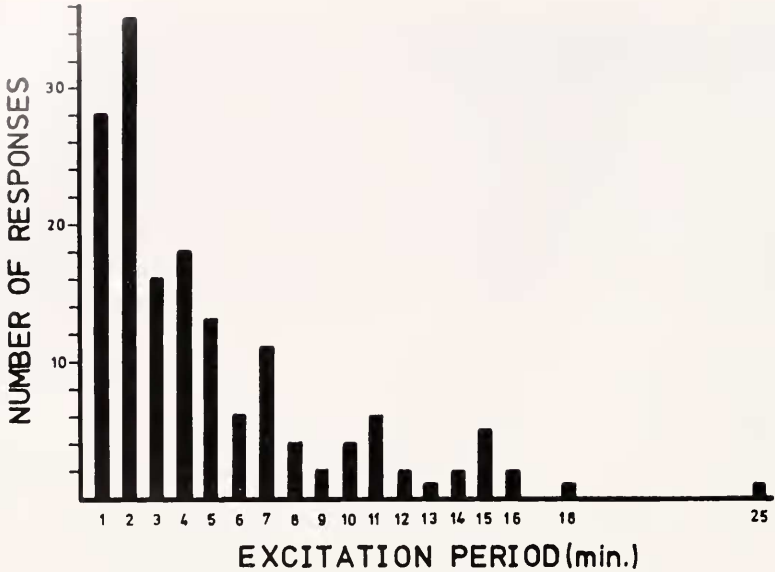


FIGURE 9. Duration of the excitation periods of 157 *A. krebsi* intraspecific acrorhagial responses. The excitation period was defined as the time from first contact of the animals to the expansion of an acrorhagus to one half the length of adjacent tentacles.

ever, there is no appreciable decrease in tentacle size and the fluid used to inflate the acrorhagi appears to come from the main coelenteron.

In most responses, application behavior immediately followed the acrorhagial expansion (Fig. 10). However, during some responses, several minutes elapsed between acrorhagial expansion and the onset of application behavior. Application behavior was never initiated during some acrorhagial responses, and in many of these instances, the tentacles and column were contracted so that the acrorhagi were prominent. Even without application, a touch of the eliciting animal to an expanded acrorhagus caused an acrorhagial peel.

As in *A. elegantissima* (Francis, 1976), the number of acrorhagi a specimen of *A. krebsi* possesses varies and is not strictly proportional to anemone size. Typically, as the application phase of the acrorhagial response progresses, more acrorhagi expand. The total number of expanded acrorhagi (usually 2-8) varies

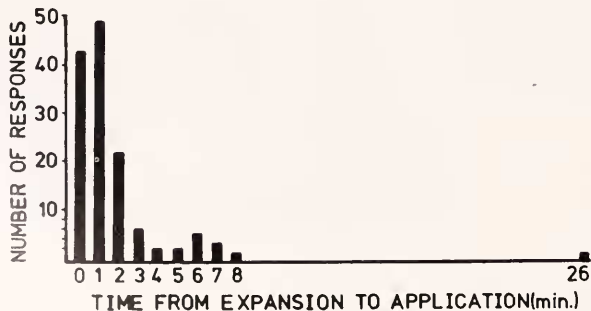


FIGURE 10. Times from acrorhagial expansion to the onset of application behavior during 134 *A. krebsi* intraspecific acrorhagial responses.

with the individual. Also, as the application progresses, the capitulum in the region of the expanded acrorhagi usually expands. Acrorhagial application is directed toward the area of stimulation. When the stimulus, either an excised tentacle or a whole anemone, was moved around a specimen of *A. krebsi*, the zone of acrorhagi expansion and direction of application followed the stimulus.

During application the expanded acrorhagi are pressed tightly against the target, in many instances for more than 30 sec. When an acrorhagus is withdrawn, a patch of the acrorhagus-tip ectoderm, the peel, remains on the target. As reported for *A. elegantissima* (Francis, 1973b) and *A. equina* (Bonnin, 1964), *A. krebsi* returns to a normal posture following the acrorhagial response. Typically, after removal of the target, the acrorhagi are applied to the former position of the target animal several times. After the application ceases, the acrorhagi usually return to their unexpanded state in approximately 10 min.

Anthopleura xanthogrammica acrorhagial response

Anthopleura xanthogrammica was previously reported to be the sole case of an acrorhagi-bearing anemone lacking an acrorhagial response (Francis, 1973b). However, *A. xanthogrammica* acrorhagial responses were observed under field conditions (Figs. 4-6). A pair of touching specimens of *A. xanthogrammica* in a small tidal pool were watched for approximately 15 min (also observed by L. Minasian and E. Conklin). When first seen, one of the anemones had expanded acrorhagi in the region adjacent to the other anemone and was in the midst of application behavior. During the observation period, the former target anemone also initiated an acrorhagial response. The response of the former aggressor then subsided. This second response continued until I left. Upon my return approximately 1 hr later, both anemones were contracted and there was no longer any contact. The *A. xanthogrammica* acrorhagial response consisted of acrorhagial expansion, application behavior, and peeling, as described for *A. equina* (Abel, 1954; Bonnin, 1964), *A. elegantissima* (Francis, 1973b), and *A. krebsi*.

Bunodosoma cavernata acrorhagial response

Bunodosoma cavernata has the previously described five phases in its acrorhagial response. However, *B. cavernata* usually maintains a different posture during the application behavior. Instead of expanding the capitulum and drawing back the tentacles in the region of acrorhagial expansion, *B. cavernata* contracts its tentacles into the oral area. This leaves the swollen acrorhagi as the sole protuberances on the upper column (Fig. 8). On other occasions, however, the *B. cavernata* application posture more closely resembles that of *A. krebsi*.

Anemonia sargassensis acrorhagial response

In laboratory studies, *Anemonia sargassensis* very seldom displayed an acrorhagial response. Usually the anemones moved away from contact with others. In the 10 observed *A. sargassensis* acrorhagial responses, the acrorhagi expanded, although generally not as much as in *B. cavernata* or *Anthopleura*. The tentacles were not retracted as much as those of *B. cavernata* and, in most cases, not even as much as the tentacles of *A. krebsi*. Application behavior was not observed in *A. sargassensis*. In all instances, when *A. krebsi* or *B. cavernata* contacted a turgid

A. sargassensis acrorhagi a peel occurred, but there was no directed application of a peel.

Effects of the peel on the target animal

Acrorhagial peels had three gross effects on both allogeneic and xenogeneic target animals: behavioral, mechanical, and necrotic. The first two effects will be discussed here. The peels of *A. krebsi*, *B. cavernata*, and *A. sargassensis* appeared to produce the same results, except the larger size of some *B. cavernata* peels magnified the effect. Anemones had three common behavioral responses to receiving a peel. Anemones receiving a peel on a tentacle, especially *A. sargassensis*, often contracted the tentacle (or tentacles) involved (Fig. 4). These tentacles remained contracted even when all the other tentacles were expanded. In some specimens of *A. sargassensis*, the affected tentacles remained contracted more than 24 hr after the application of a peel. After several peels, the anemones usually released their hold on the substrate and under field conditions would have been washed away. Upon receiving peels, specimens of *A. krebsi* commonly contracted, and using the pedal disc, moved away. On several occasions, large peels bound the tentacles or acrorhagi of a target anemone together, causing a mechanical impediment to their normal use. In three cases, 24 hr after an application the tentacles were still bound together.

Acrorhagial response specificity

To test the specificity of the acrorhagial response, various objects were applied with the 1-sec touch technique to *B. cavernata* tentacles. In five trials, glass coverslips, *Artemia*-extract-coated coverslips (which elicited nematocyst discharge from the tentacles), a stainless steel probe, and previously excised tentacles from the opposite side of the test anemone, all failed to elicit expansion or application behavior. Following each failure, an acrorhagial response was elicited from the specimens of *B. cavernata* by an excised *A. sargassensis* tentacle.

As with *A. krebsi* (Bigger, 1976), the specificity of acrorhagial peeling was tested in *B. cavernata* and *A. sargassensis*. An excised tentacle of *A. krebsi* was used to elicit an acrorhagial response from *B. cavernata*; then, following an acrorhagial peel, the excised tentacle was removed. A previously excised tentacle from the *B. cavernata*, a glass coverslip, and an *Artemia*-extract-coated coverslip were each touched ten times to expanded acrorhagi. In ten trials, they did not elicit a peel. The excised *A. krebsi* tentacles were then again touched to expanded acrorhagi and, in all instances, a peel resulted from the first contact. The same protocol was used in five trials with *A. sargassensis* and the same results were obtained.

Response threshold change

The acrorhagi expansion and acrorhagial application thresholds of *A. krebsi* were determined for repeated responses to see if either habituation or sensitization occurred. The response of *A. krebsi* to *C. gigantea* tentacles was tested at 10-min intervals with the 1-sec touch technique. The *A. krebsi* response to *A. sargassensis* tentacles was likewise tested for 15-, 30-, 60-, and 120-min intervals. In all cases (Fig. 11), there was a rapid decrease in threshold for the second set of stimulations. With 15-, 30-, 60-, and 120-min intervals, the threshold remained low. After 60 min of stimulation at 10-min intervals, some specimens of

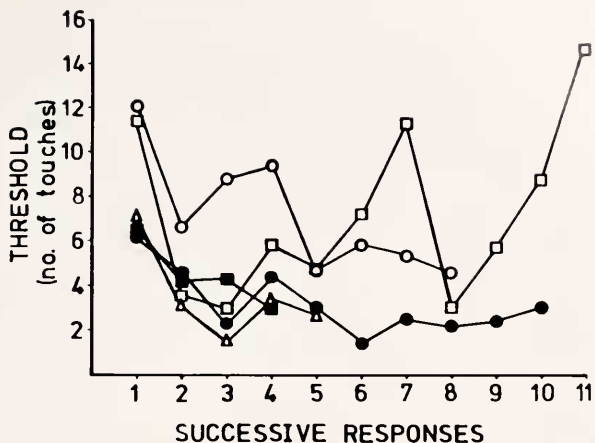


FIGURE 11. Changes in *A. krebsi* acrorhagial response with elicitation at intervals of 10–120 min. Using the 1-sec touch technique with excised *C. gigantea* (10 min) and *A. sargassensis* (15–120 min) tentacles, acrorhagial responses were elicited from *A. krebsi* at various time intervals. The threshold was defined as the number of touches required for acrorhagial expansion. The average thresholds of 10 individuals for each time interval are displayed in this graph. Open box = 10 min, closed circle = 15 min, open circle = 30 min, open triangle = 60 min, and closed box = 120 min.

A. krebsi would not respond. In most cases, the anemone would respond during the following stimulation periods. The time of these refractory periods varied among the anemones tested. Following the fifth stimulation period, some of the test anemones were in a refractory period and some were responding normally. This variability is responsible for the high values in the later part of the 10-min-interval curve in Figure 11.

In this study, the effect of size on the acrorhagial response was not specifically studied. Specimens of *Anthopleura krebsi* of approximately the same size were paired in most intraspecific interactions. However, in three cases groupmates of various size were tested against the same target animals. The groupmate/target size ratios for individuals in the three groups were: 1) 3 of 1:1, 1 of 2:3, and 2 of <1:2; 2) 2 of 1:1, 2 of 2:3, and 2 of <1:2; 3) 1 of 1:1 and 1 of 3:2. In these tests, the combination rather than size was the best correlate of which anemone was first to respond, i.e., all individuals of a group performed the same with the same target animal. In the field, specimens of *A. krebsi* have been observed to initiate an acrorhagial response to larger nonresponding non-groupmates, but the prior history of pairs was unknown and controls were lacking. In *A. krebsi*/*B. cavernata* interactions, *A. krebsi* usually responded before the much larger *B. cavernata*; however, upon receiving *B. cavernata* peels (one application could cover a large portion of the *A. krebsi*) the *A. krebsi* always ceased its attack and contracted.

Interspecific acrorhagial responses

The response of *A. krebsi* to *Bunodosoma granulifera* was tested with the 1-sec touch technique using intact *B. granulifera* tentacles as the stimulus. An acrorhagial response, including peeling, was elicited from *A. krebsi* in all three trials. Each interspecific interaction between *B. cavernata* or *A. sargassensis* and a variety

TABLE I

The interspecific nature of the *Bunodosoma cavernata* acrorhagial response. The number of 1-hr interactions between a *B. cavernata* and a test animal is given in parentheses. Key: + = the response in question was elicited; - = the response in question was not elicited.

Test animal	<i>B. cavernata</i> acrorhagial expansion	<i>B. cavernata</i> application behavior	<i>B. cavernata</i> acrorhagial peel
Anthozoa			
<i>Anthopleura krebsi</i>	+ (5)	+ (5)	+ (5)
<i>Anemonia sargassensis</i>	+ (5)	+ (5)	+ (5)
<i>Calliactis tricolor</i>	+ (2), - (1)	+ (2), - (1)	+ (2), - (1)
<i>Condylactis gigantea*</i>	- (2)	- (2)	- (2)
<i>Bunodosoma granulifera</i>	+ (2), - (1)	+ (2), - (1)	+ (2), - (1)
Hydrozoa			
<i>Campanularia</i> sp.	- (5)	- (5)	- (5)
Non-coelenterates			
<i>Pagurus longicarpus</i> (hermit crab)	- (5)	- (5)	- (5)
<i>Pagurus pollicaris</i> (hermit crab)	- (5)	- (5)	- (5)
<i>Spurilla neapolitana</i> (nudibranch)	- (5)	- (5)	- (5)

* Test animals were ingested by the specimen of *B. cavernata*.

of animals was observed for 1 hr to determine how extensively the acrorhagial response occurred in interspecific encounters (Tables I and II). The results followed the same pattern as in earlier reports on *A. equina* (Bonnin, 1964), *A. elegantissima* (Francis, 1973b) and *A. krebsi* (Bigger, 1976). Sea anemones usually elicited an acrorhagial response from *B. cavernata*, whereas hydroids and

TABLE II

The interspecific nature of the *Anemonia sargassensis* acrorhagial response. The number of 1-hr interactions between a specimen of *A. sargassensis* and a test animal is given in parentheses. Key: + = the response in question was elicited; - = the response in question was not elicited.

	<i>A. sargassensis</i> acrorhagial expansion	<i>A. sargassensis</i> application behavior	<i>A. sargassensis</i> acrorhagial peel
Anthozoa			
<i>Anthopleura krebsi*</i>	+ (2), - (3)	- (5)	+ (2), - (3)
<i>Bunodosoma cavernata</i>	+ (1), - (4)	- (5)	+ (1), - (4)
<i>Bunodosoma granulifera</i>	- (3)	- (3)	- (3)
<i>Calliactis tricolor*</i>	- (5)	- (5)	- (5)
<i>Bunodactis texensis*</i>	- (3)	- (3)	- (3)
Hydrozoa			
<i>Campanularia</i> sp.	- (5)	- (5)	- (5)
Non-coelenterates			
<i>Pagurus longicarpus</i> (hermit crab)	- (5)	- (5)	- (5)
<i>Pagurus pollicaris</i> (hermit crab)	- (5)	- (5)	- (5)
<i>Spurilla neapolitana</i>	- (5)	- (5)	- (5)

* Specimens of *A. sargassensis* usually avoided contact with the test animal (discussed in text).

non-coelenterates did not. The *A. sargassensis* used in this study tended to avoid contact rather than to employ the acrorhagial response against coelenterates and showed no acrorhagial response toward non-coelenterates.

Bigger (1976) reported the only observations of a non-anthozoan (scyphozoan) eliciting an acrorhagial response. *Anthopleura krebsi* acrorhagial responses were elicited during two of three encounters with *C. xamachana* scyphistomae. Surprisingly, the *Cassiopea* medusae in that study did not elicit an acrorhagial response from *A. krebsi*. The medusae and scyphistomae had been collected at different geographical locations and the species identification of the polyp was uncertain (later confirmed as *Cassiopea xamachana*).

To further examine those reported differences in *A. krebsi*'s response to *Cassiopea xamachana* medusae and scyphistomae, 64 1-sec touch tests were performed with scyphistomae and 42 tests with medusae (Table III). To eliminate possible genetic differences, all of the polyps and medusae were from the same clone (raised from a single polyp). Approximately the same percentage of *C. xamachana* polyps and medusae elicited acrorhagial expansion from *A. krebsi*. The percentage of medusae eliciting the application behavior was about half that of the polyps. Most important, all of the polyps that elicited acrorhagial expansion elicited an acrorhagial peel. None of the medusae elicited a peel, even when touched 15-30 times to an expanded acrorhagus.

Intraspecific interactions in A. krebsi

In order to test an intraspecific competition model proposed for the acrorhagial response by Francis (1973b), as well as the more general competition models (Jackson and Buss, 1975; Connell, 1976), the interactions of seven groups of *A. krebsi* were examined in a series of 1-hr observations. The groups were from sites 60 cm to 250 m apart (separated by sand). The study groups consisted of five groups of the red color morph and two of the green. The groups were maintained in separate bowls and, in these observations, one anemone of a combination was moved (on its shell) to the bowl of the other group and placed so that reexpansion of its tentacles forced tentacle contact with one of the residents. The water was not changed prior to the interaction period. The combinations were planned as a 7×7 matrix with four replicates so that an anemone of each group was introduced into the bowl of every other group four times, and vice versa.

TABLE III

Response of Anthopleura krebsi to contact with Cassiopea xamachana. Whole animals or, in some cases, excised medusae oral arms were applied to A. krebsi tentacles with the 1-sec touch technique. When acrorhagial expansion was elicited, the stimulus was applied to an expanded acrorhagus for at least 1 sec, 15 times.

Cassiopea	Polyps	Medusae
No acrorhagial response	45 (70%)	28 (67%)
Acrorhagial response	19 (30%)	14 (33%)
Acrorhagial expansion	19 (30%)	14 (33%)
Application behavior	19 (30%)	7 (17%)
Peel Produced	19 (30%)	0
Total tested:	64	42

TABLE IV

Relative aggressiveness of seven A. krebbsi groups. As explained in detail in the text, each block of the matrix represents the results of eight 1-hr interactions of that combination. The set of interactions for each group pairing was scored for each group: moving away—1, contracting—2, receiving peels but remaining in place—3, remaining in place while the other anemone contracts or moves away—4, initiating the acrorhagial response and placing peels on the other anemone—5, no response during any of the interaction—NR. Total score for the horizontal group was subtracted from the diagonal group to obtain a measure of the relative aggressiveness of the groups; i.e., 0—both groups of a combination were equally aggressive, “-” score—the horizontal group was the more aggressive of the pairing, and “+” score—the diagonal group was the more aggressive of the pairing.

	8cl	4dl	5ea	62	6c	3e	2e
8cl	NR	-16	-12	-6	-2	0	+14
	4dl	NR	-10	-9	-8	-4*	0
		5ea	NR	NR	NR	NR	NR
			62	NR	NR	NR	NR
				6c	NR	NR	NR
					3e	NR	NR
						2e	NR

* Score based on only four interactions.

One group died of causes unrelated to the study toward the end of this investigation, leaving one combination and its reciprocal with four observations.

An anemone of each group was also removed and reintroduced to its groupmates ($4 \times$). No groupmates responded. The red groups never responded to another red group but did have acrorhagial responses to both green groups. The green groups directed acrorhagial responses toward each other and most red groups. Some intergroup combinations consistently resulted in the same group initiating an acrorhagial response, but in others the initiating group varied. Distance between the paired groups in the field did not seem to be an indicator of the outcomes of those interactions. In 25% of the interactions involving an acrorhagial response, both anemones initiated a response.

The outcome of each interaction was scored in terms of aggressiveness for each member of the anemone pairs (Table IV). For each combination of two groups, one group's score was subtracted from the other group's score and divided by the number of interactions for each combination to give a measure of the relative aggressiveness of the two groups under those conditions.

Whether anemones were introduced or were residents in the interactions did not significantly (Wilcoxon signed-rank test) affect the outcome. Therefore, all interactions (8) of each group combination are combined and given in Table IV as a relative measure of the aggressiveness of the responsive groups.

DISCUSSION

The discovery of such a complex behavior as the acrorhagial response in the morphologically relatively simple actinians has raised a number of questions. What

is the behavioral nature of the response? What animals will elicit the response? Do factors such as prior experience, relative size, residence, and genotype of the interacting anemones affect the outcome? What is the functional significance of the response? Is the acrorrhagial response related to other coelenterate self/not-self recognition systems or to an immune system?

Despite an earlier report to the contrary (Francis, 1973b) and a single observation under unusual circumstances (Lindberg, 1976) the current study presents an observation of *A. xanthogrammica* displaying an acrorrhagial response under field conditions, so that all anemones with acrorrhagi that have been examined are known to display a similar acrorrhagial response (Abel, 1954; Bonnin, 1964; Francis, 1973b; Bigger, 1976). As pointed out by Francis (1973b) the acrorrhagial response meets the general definition of an aggressive behavior. Some definitions (*e.g.*, Hinde, 1970) require an aggressive behavior to be directed towards the other individual, a criterion met by the application component of the acrorrhagial behavior of all species examined except *A. sargassensis*. Even in that instance, one can make a case for the directed nature of the *A. sargassensis* acrorrhagial response because the specificity of the peeling insures a directed nature; *i.e.*, the response can only go to completion upon contact with the proper animal. Of special interest is the fact that anemones will respond to the same species as food or as an acrorrhagial target, but at different times. Although there is a fine line between predation and aggression, in some cases, (*i.e.*, in corals, Lang, 1971 and 1973) the same phenomenon might be considered as both. Because predation and the acrorrhagial response are mutually exclusive, one need only consider the acrorrhagial response in terms of aggression.

Bonnin (1964) demonstrated that induction of an acrorrhagial response in *A. equina* caused a lowering of the threshold for subsequent acrorrhagial responses elicited at 10-min intervals, and that by the sixth acrorrhagial response specimens of *A. equina* became unresponsive to further stimulation. In the present study, a similar threshold lowering and elevation was observed when the *A. krebsi* acrorrhagial response was elicited at 10-min intervals. However, not all specimens of *A. krebsi* became totally refractory and at longer intervals between response elicitation (15+ min), the *A. krebsi* acrorrhagial response threshold remained low (Fig. 11). In *A. krebsi*, prior experience influenced later responses over periods as long as 2 hr; this should be considered in experimental design.

Acrorrhagial responses have not been elicited by non-coelenterates in the five anemone species that have been examined: *A. equina* (Bonnin, 1964), *A. elegantissima* (Francis, 1973b), *A. krebsi* (Bigger, 1976), *A. sargassensis* and *B. cavernata* (this study). Therefore, these sea anemones must compete with non-coelenterates for resources in some other fashion. To date (Abel, 1954; Bonnin, 1964; Francis, 1973b; Bigger, 1976), acrorrhagial responses have only been elicited by some sessile anthozoans or *C. ramachana*. Past consideration of the role of the acrorrhagial response has emphasized intraspecific interactions on the grounds that those were much stronger than the interspecific acrorrhagial responses (Francis, 1973b). The highly predictable, full acrorrhagial responses of either *A. krebsi* or *B. cavernata* to *A. sargassensis* indicate that acrorrhagial responses could be effectively employed against some other anthozoans, but the lack of pertinent field data limits a full assessment of the interspecific role of the acrorrhagial response.

This study amplifies the preliminary report (Bigger, 1976) of a difference in the response of *A. krebsi* to polyps and medusae of the scyphozoan *C. ramachana*. With twice the effectiveness of the medusa in soliciting acrorrhagial application, the polyp appears either to have a qualitatively more effective application-eliciting

factor or to contain more of the eliciting factor. In the light of Bonnin's suggestion (1964) that the nematocysts of the target animal constitute the eliciting factor, it should be noted that the nematocysts of polyp tentacles and medusa mouth fronds (an area that touched the anemones) are morphologically the same and appear to be present in roughly equivalent numbers (Mariscal and Bigger, 1976; unpublished observations). Nematocyst toxins from *Cassiopea* medusae and scyphistomae have not been compared. For the most important measure of the responses, peel elicitation, 30% of the polyps, but never the medusae, elicited peels. These results point out the separation between the acrorhagial response components (acrorhagial expansion, application behavior, and ectodermal peeling; see Bigger, 1976) and suggest three possibilities: 1) Each component may require a different eliciting factor (or combination of factors). The medusae and polyps would contain the expansion factor but differ in their complement of other factors. 2) The receptors for the three components may have different thresholds for the same factor. The medusae and polyps would have enough of the eliciting factor to exceed the acrorhagial expansion threshold but would be quantitatively differentiated by the receptors of the other two components. 3) The discrimination would be based on some combination of the first two. At this time there are not enough data to suggest one possibility more than another.

Francis (1973b) proposed that the acrorhagial response primarily functioned in intraspecific competition for space. Central to Francis' hypothesis is the concept that anemones distinguish clonemates from all other conspecifics, a concept derived from observations of *A. elegantissima* acrorhagial responses being elicited by all non-groupmates ("non-clonemates"). This study shows that not all *A. krebsi* non-groupmates elicit a response. In fact, some specimens of *A. krebsi* with different color morphs, one of Francis' criteria for non-clonemates, did not respond to each other. Therefore, one cannot consider the acrorhagial response to be solely a case of an "individual" (clone) recognizing all other conspecifics as not-self and competing with them for available space. One must examine this as a case of related individuals (individual = clone) competing for space. These related individuals share alleles at some loci, which may include those determining surface molecules that participate in the recognition events of the acrorhagial response. The difference between the acrorhagial interaction of all *A. elegantissima* groups (Francis, 1973b) and the intergroup compatibility of some *A. krebsi* groups could reflect a true species difference or, alternatively, a more homogeneous gene pool in the specimens of *A. krebsi* sampled, such as the extremely limited or homogeneous gene pool in the Maine population of the sea anemone *Haliplanella luciae* (Schick, 1976). The data of Francis (1973b) and this study demonstrating the wide number of conspecific groups recognized by *A. elegantissima* and *A. krebsi* and the variability of the *A. krebsi* acrorhagial responses suggest multiple alleles coding for acrorhagial recognition and perhaps many different loci, *i.e.*, a complex polygenic phenomenon such as the mammalian histocompatibility system.

There is also a major genetic influence in other coelenterate self/not-self recognition systems, *e.g.*, overgrowth in hydroids (Ivker, 1972) and histoincompatibility in corals (Hildemann *et al.*, 1977) and gorgonians (Theodor, 1970). Thus reports of various factors, *e.g.*, size (Brace and Pavey, 1978), controlling the initiation of an acrorhagial response must be viewed with caution unless the genetic variable is controlled. Because there are no inbred strains, this is difficult with a solely sexually reproducing anemone. Asexually reproducing anemones such as *A. elegantissima* and *A. krebsi*, on the other hand, present the investigator with

a large number of genetically identical anemones which allow reproducible group combinations under a variable experimental condition. Brace and Pavey (1978) reported a size hierarchy in the initiation of the acrorhagial response of *A. equina* (a solely sexually reproducing anemone), the larger anemones being first to respond. However, in approximately one third of the interactions of their study the smaller anemone was faster or as fast to initiate an attack. This indicates that other factors should be considered. Very limited evidence concerning the influence of size on the initiation of acrorhagial responses in *A. krebsi* suggests that size plays at most a subordinate role to the particular group combination ("histoincompatibility differences") in that species. The current study also suggests that residence in an area does not influence the outcome of *A. krebsi* interactions. Because the test anemones of this study were moved while still attached to their shells, the experimental design only allowed residence to be considered in terms of the anemone's surroundings and not on the basis of pedal attachment. Ottaway (1978), in his recent field observations of *Actinia tenebrosa*, noted "the successful aggressor was almost invariably the 'defender,' the anemone that had been stationary at the time of contact." Therefore, although general surroundings may not significantly influence the acrorhagial response, movement or long-term attachment may affect outcome.

If the acrorhagial response functions in competition for space, as proposed by Francis (1973a and b, 1976), one needs to explain coexistence of competitive groups. Several models for invertebrate competitive or aggressive interactions have been used to discuss interspecific situations (e.g., Lang, 1973; Jackson and Buss, 1975; Connell, 1976). A hierarchy of aggression among corals has been reported by Lang (1971 and 1973). Connell (1976) suggested that such linear hierarchies are inherently unstable and that the intervention of an outside force that selectively acted against the higher ranked members of the hierarchy could explain the concurrent existence of all the groups. Jackson and Buss (1975) and Buss (1976) proposed an interaction model of "competitive networks" rather than a linear dominance, i.e., $A > B > C > A$, etc. Brace and Pavey (1978) reported such a "ring" situation in *A. equina* acrorhagial interactions and Table IV of the present study reveals one such network in *A. krebsi* interactions. However, contrary to the results of Brace and Pavey (1978) with *A. equina*, Table IV of this study indicates a high degree of variability in the outcomes of interactions between certain combinations of *A. krebsi*. Connell (1976) found the same variable outcomes in tissue destruction and overgrowth among the corals he studied. Buss (1976) states that such competitive networks function by increasing the time required for a dominant to be established and thereby reduce the magnitude of a disturbance required to maintain diversity. Rather than the acrorhagial response being viewed in a limited sense as only the mechanism whereby a clone can capture territory from conspecific competitors, the acrorhagial response can be viewed as one of a set of ecological factors possibly maintaining a heterogeneous gene pool and, through indirect interactions with other ecological factors, causing an optimal utilization of available space.

Hildemann and his associates (1975) specifically included the acrorhagial response when they categorized what they felt were four levels of "immunoreactivity" in coelenterates. In discussing the acrorhagial response, they recognized that a response elicited within minutes after first contact could represent non-immunological recognition but went on to suggest that because the anemones live in a crowded habitat, prior sensitization was not ruled out. Bigger (1976)

reported the rapid elicitation of acrorhagial responses from *A. krebsi* by several allopatric species, including *Condylactis gigantea*, *C. ramachana*, and *Cerianthopsis americanus*. A possible explanation, consistent with an immunological mechanism, for the rapid response to allopatric species would be that those allopatric target animals possessed a set of surface molecules so similar to those of previously encountered target animals that the two sets of molecules were perceived as the same. However, the concept of prior sensitization as a basis for the rapidity of the acrorhagial response must be viewed with certain reservations.

More recently (Hildemann *et al.*, 1979), it has been suggested that three minimal criteria must be met for a phenomenon to be considered immunologic: cytotoxic or antagonistic reactions, selective or specific reactivity, and inducible memory or selectively altered reactivity on secondary contact. Thus, while self/not-self recognition is certainly the cornerstone of immunology, not all self/not-self phenomena are immunologic in nature. Reactions among coelenterates involving self/not-self recognition include various cellular and behavioral phenomena in hydroids (Kato *et al.*, 1967; Ivker, 1972), gorgonians (Theodor, 1970; Bigger and Runyan, 1979), corals (Lang, 1971; Hildemann *et al.*, 1977), and sea anemones (Abel, 1954; Purcell, 1977). While all the above coelenterate responses might be considered to meet the first two criteria for an immune response, experiments examining the third criterion have been performed only with corals. Although Hildemann *et al.* (1977) demonstrated the characteristics of an immune system in corals, little is known about the recognition mechanisms, receptors, or molecular pathways involved, nor in some cases the effector cell types in the above mentioned coelenterate reactions. Until such information is acquired, suggestions of a common underlying recognition mechanism remain speculative. That the acrorhagial response utilizes a behavioral effector component does not preclude the use of a recognition system similar to that of other coelenterate self/not-self or immunological phenomena. However, the nature of the recognition along with many other questions about the functioning of the effector side of the acrorhagial response must await future investigations.

Dr. R. N. Mariscal's advice during this study and his critical reading of a preliminary draft of this manuscript were greatly appreciated. Thanks are also due Dr. W. H. Hildemann for critically reading this manuscript and offering valuable suggestions, Dr. M. J. Greenberg for suggestions, Dr. W. Herrnkind and the FSU Psychobiology Program for the loan of equipment, Steve White for statistical assistance, and Lois Bigger for translations. Some financial support for this study was provided by NSF Grant #DEB 77-22148 to Dr. R. N. Mariscal. Portions of this paper were submitted to Florida State University in theses in partial fulfillment of the requirements for the degrees of M.S. and Ph.D. This is contribution number 143, Tallahassee, Sopchoppy, and Gulf Coast Marine Biological Association.

SUMMARY

The acrorhagial responses of four sea anemones, *Anthopleura krebsi*, *Bunodosoma cavernata*, *Anemonia sargassensis*, and *Anthopleura xanthogrammica*, are described. All four acrorhagial responses can be considered forms of aggression. The acrorhagial response is only one of several responses of sea anemones to contact with other animals: others include several methods of avoidance and feeding.

Prior experience can influence the acrorrhagial response. In *A. krebsi*, the effect of a prior encounter on the excitation threshold can be seen for at least 2 hr.

Interspecific behavioral interactions were examined in *A. krebsi*, *B. cavernata*, and *A. sargassensis*. With one exception, acrorrhagial responses were only elicited by contact with some anthozoans. The exception is that some *A. krebsi* respond to the scyphistomae of the scyphozoan *Cassiopea xamachana*. Some *C. xamachana* medusae from the same clone also elicited acrorrhagial expansion and application behavior but never acrorrhagial peeling.

Intraspecific interactions were examined in *A. krebsi*. Clonemates and group-mates never elicited acrorrhagial responses from one another. Some non-group-mates, including different-colored groups, did not respond to one another and in some other group combinations the interactive outcome was variable. It is suggested the acrorrhagial response involves multiple alleles and perhaps involvement of different loci coding for cell-surface recognition molecules. Several competition models were examined for these intraspecific interactions. An intergroup linear hierarchy was not found.

The acrorrhagial response is certainly an example of self/not-self recognition. This response has exquisite specificity and leads to cytotoxic effects. It cannot at this time be considered immunological.

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